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Alien interference: Disruption of infochemical networks by invasive insect herbivores

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ABSTRACT

Insect herbivores trigger various biochemical changes in plants and, as a consequence, affect other organisms that are associated with these plants. Such plant-mediated indirect effects often involve herbivore-induced plant volatiles (HIPVs) that can be used as cues for foraging herbivores and their natural enemies, and are also known to affect pollinator attraction. In tightly co-evolved systems, the different trophic levels are expected to display adaptive response to changes in HIPVs caused by native herbivores. But what if a new herbivore invades such a system? Current literature suggests that exotic herbivores have the potential to affect HIPV production, and that plant responses to novel herbivores are likely to depend on phylogenetic relatedness between the invader and the native species. Here we review the different ways exotic herbivores can disrupt chemically mediated interactions between plants and the key users of HIPVs: herbivores, pollinators, and members of the third (i.e. predators and parasitoids) and fourth (i.e. hyperparasitoids) trophic levels. Current theory on insect invasions needs to consider that disruptive effects of invaders on infochemical networks can have a short term impact on the population dynamics of native insects and plants, as well as exerting potentially negative consequences for the functioning of native ecosystems.

Key-words: invasive species, plant volatiles, multitrophic interactions, plant-insect interactions

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INTRODUCTION

Plant volatiles are of key importance for the foraging behaviour of many insects. Pollinators, for example, use plant-produced volatiles to locate rewarding flowers (Pichersky & Gershenzon, 2002, Raguso, 2008, Schiestl, 2010). In contrast to these mutualists, many herbivores utilize plant volatiles to identify suitable host plants (Bruce, Wadhams & Woodcock, 2005). Of particular interest is the phenomenon that plants under attack by arthropod herbivores show dramatic increases in the production of specific volatiles. Certain herbivores are deterred by these inducible volatiles (De Moraes, Mescher & Tumlinson, 2001, Kessler & Baldwin, 2001), possibly to avoid competition, reduced food quality, or natural enemies, but others are attracted to already infested plants (Heil, 2004, Horiuchi, Arimura, Ozawa, Shimoda, Dicke, Takabayashi & Nishioka, 2003), in certain cases to initiate mass attacks on weakened hosts (Raffa, Phillips & Salom, 1993).

Inducible plant volatiles are also of great importance to predators and parasitoids in search of prey or hosts. Therefore, herbivore-induced plant volatiles (HIPVs) are proposed to function as a form of indirect resistance that relies on the third trophic level to reduce herbivore damage (Dicke & Sabelis, 1988, Turlings, Tumlinson & Lewis, 1990). This indirect defensive function is still highly debated (Allison & Hare, 2009, Arimura, Matsui & Takabayashi, 2009, Hare, 2011, Heil & Karban, 2010, Holopainen, 2004, Peñuelas & Llusià, 2004), but there is an overall consensus that arthropods at different trophic levels use plant volatiles to locate key resources and that these chemically-mediated interactions may be very specific, with each species having evolved to exploit particular volatile blends. We propose that invading insect herbivores

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may disrupt these finely-tuned chemically mediated interactions and that this may have consequences for the reproductive success and eventually the population structure of the interacting native plants and insects.

With increasing globalization, many plants and animals are being accidentally or intentionally introduced into non-native ecosystems, and some of these invaders pose major threats for biodiversity and the functioning of ecological processes in their introduced range (Gandhi & Herms, 2010, Vilà, Espinar, Hejda, Hulme, Jarošík, Maron, Pergl, Schaffner, Sun & Pyšek, 2011). Moreover, recently observed changes in climate that are driven largely by humans are also challenging species to adapt and many are responding by moving polewards. The consequences of these invasions have been studied extensively, but very little attention has been given to many important mechanisms involved, such as plant odour-mediated interactions (Gandhi & Herms, 2010, Kenis, Auger-Rozenberg, Roques, Timms, Péré, Cock, Settele, Augustin & Lopez-Vaamonde, 2009). In the context of a EUROCORE project we recently launched a collaborative effort to study this concept of alien herbivores interfering with infochemical networks (Fig. 1). We particularly focus on quantifying the effects of invasive insect herbivores on the foraging behaviour of native herbivores and plant mutualists, such as pollinators and parasitic wasps. To our knowledge, no study has specifically addressed this issue, but a number of investigations on the interactions among assemblages of native arthropods (Bukovinszky, Poelman, Kamp, Hemerik, Prekatsakis & Dicke, 2012), or between native arthropods and invasive plants (Harvey & Fortuna, 2012) strongly suggest that the disruption of plant–odour mediated interactions can have ecological consequences (Table 1). Within this framework, a key point to address is whether and how the effects of exotic herbivores on HIPVs differ from effects caused by native herbivores. Indeed, native species can also play the role of

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97 "info-disrupter" in interactions within native communities. For example, the effect of
98 *Mamestra brassicae*, a Eurasian moth, on the volatiles emitted by crucifers was shown to
99 influence the outcome of the interactions between another native herbivore, *Pieris*
100 *brassicae*, and its parasitoid *Cotesia glomerata* (Bukovinszky *et al.*, 2012). Thus,
101 demonstrating that invasive species have an impact on infochemical networks may not
102 be a sufficient conclusion: the ultimate ecological challenge is to determine whether or
103 not the impact of invaders is greater than or different from the impact naturally caused
104 by other members of the native fauna, and poses a greater threat to the functioning of
105 native ecosystems. In this context, a comparative approach would be most appropriate.
106 Studying single pairs of organisms (one native species/one exotic species) may be a
107 valuable approach in a specific context, for example predicting the outcome of the
108 association between a threatening invasive species and a particularly rare or
109 ecologically important native species. However, to reveal general ecological trends and
110 to answer the question of the global impact of invasive species on infochemical
111 networks, a standardized comparison of the effects of several native and exotic species
112 on chemically mediated interactions will be necessary.
113 Two fundamental questions pertain to the notion of interference of chemically
114 mediated interactions by invasive insect herbivores: 1) how do plants perceive and
115 respond to "novel" herbivory? And 2) are insects that rely on infochemical networks
116 adapted to variations in HIPVs and able to cope with those induced by invasive
117 herbivores? Here we combine our current knowledge of biochemical mechanisms
118 involved in the production of plant volatiles and recent invasion biology literature to
119 unite/bridge both questions. Then, we address the question of adaptation to variation in
120 HIPVs for each of the trophic levels involved in infochemical networks: herbivores,

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natural enemies of herbivores (third trophic level) and their own natural enemies (i.e. hyperparasitoids, fourth trophic level), and pollinators.

HOW DO PLANTS PERCEIVE AND RESPOND TO "NOVEL" HERBIVORY?

The notion of novel herbivory, hereby defined as feeding by an herbivore that the plant has not experienced over evolutionary time, is relative. Due to the immense variety of herbivores attacking plants worldwide and the diversity of feeding strategies they occupy, the possibility of an invasive insect attacking and damaging native plants in an entirely novel way is unlikely. Geographically isolated environments, such as islands, where plants could have existed in absence of some specific guilds of herbivores (Reaser, Meyerson, Cronk, De Poorter, Eldrege, Green, Kairo, Latasi, Mack & Mauremootoo, 2007), may be an exception to that rule, but in the vast majority of exotic insects invasions, the invader will become an additional species integrated into native plant-insect food webs. Still, the scenario of an invasive species attacking native plants in the exact same way as a native herbivore is equally unlikely, because modes of feeding vary tremendously from species to species. Preferences for specific plant tissues or organs, feeding patterns, activity rhythms and circadian cycles, solitary or gregarious feeding behaviours, chemistry of saliva, and counter-adaptations to plant defences are among the many parameters that potentiate species-specific variation. In other words, all exotic herbivores are expected to have some "elements of novelty", i.e. diverge from existing native herbivores in some specific traits, but none, or very few, will pose an entirely new threat to native plants. The true question is to know which herbivore traits are fundamental to the perception by the plant of herbivory and its response in the form

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of a volatile blend emitted upon attack, and how these traits are expected to differ between native and exotic herbivores.

Herbivore cues recognized by plants

In order to investigate whether or not plant responses to exotic herbivores may differ from responses to native herbivores, we must first understand how plants perceive herbivorous arthropods, a topic that has been the subject of several recent reviews (Hilker & Meiners, 2010, Mithöfer & Boland, 2012, Mumm & Dicke, 2010, Wu & Baldwin, 2010). It is well known that plants typically produce different blends of HIPVs when damaged by insects compared to plants that are merely mechanically wounded, implying the existence of insect-derived compounds (including plant compounds modified by insect enzymes) responsible for initiating specific plant responses. Such elicitors have been discovered in insect oral secretions for several systems (Pare, Farag, Krishnamachari, Zhang, Ryu & Kloepper, 2005, Tumlinson & Engelberth, 2008). Additionally, plants can perceive other types of insect cues, related to touch (Hall, MacGregor, Nijsse & Bown, 2004), or associated with oviposition (Reymond, 2013). Plant responses to oviposition-related elicitors range from direct defence [e.g. necrosis, growth of undifferentiated wound tissue (Balbyshev & Lorenzen, 1997, Desurmont & Weston, 2011)] to the production of specific HIPV blends attractive to natural enemies (Fatouros, Bukovinszkine'Kiss, Dicke & Hilker, 2007).

While critical for plant responses, biochemical elicitors do not constitute the only facet of herbivory. The type of damage inflicted to the plant is also known to influence the production of plant volatiles. Sucking piercing insects such as aphids induced different responses than chewing insects such a caterpillars (Bidart-Bouzat & Kliebenstein, 2011). Also the location (i.e. organ attacked) and the "physical

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characteristics" (e.g. scratching, chewing, or skeletonizing damage for leaf-feeders) of the damage may matter and result in the production of distinct blends of HIPVs (Mithöfer & Boland, 2008, Pierre, Jansen, Hordijk, van Dam, Cortesero & Dugravot, 2011). This matter is complicated by the fact that feeding habits can be plastic and change over the lifetime of an herbivore, as illustrated by *P. brassicae* caterpillars, which are typically leaf feeders but switch to flower-feeding during their development on *Brassica nigra* (Smallegange, Van Loon, Blatt, Harvey, Agerbirk & Dicke, 2007). Finally, plants can respond to the time course and circadian rhythm of herbivory (Arimura, Köpke, Kunert, Volpe, David, Brand, Dabrowska, Maffei & Boland, 2008, Connor, Rott, Samietz & Dorn, 2007, Mithöfer, Wanner & Boland, 2005). These results suggest that the production of specific volatile blends in response to herbivory can be, in certain cases, independent of the presence of elicitors in oral secretions. However, from the plant's perspective, feeding habits may be less reliable of the identity of an attacker than biochemical elicitors due to their potentially variable and dynamic nature.

In summary, we postulate that the volatile blend produced by a plant in response to herbivory can depend on three herbivore-dependent variables: 1) the type of elicitors associated with the herbivore, 2) the type and location of damage inflicted to the plant, and 3) the time course or rhythm of herbivory. Because tremendous variation in these traits exists among potential invasive insect herbivores, making general predictions about the extent to which plant responses to exotic and native herbivores may differ in general is a seemingly impossible task. Practically, in order to predict how a plant will respond to a given exotic species, it is necessary to examine where the novel herbivore is situated within this space of the tripartite herbivory traits, or, in other words, determine its coordinates on a three-dimensional "herbivory map", and compare these coordinates to those of the assemblage of native herbivores associated with the plant.

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195 This trait-matching approach has been used in invasion biology studies, mainly in the
196 context of predicting the native species of herbivores most likely to feed on an exotic
197 plant, and evaluating the risks of non-target effects on native plants following the
198 introduction of a biological control agent of an exotic plant (Pearse, Harris, Karban & Sih,
199 2013). However, the principal limitation of such approaches is the lack of detailed
200 information available on the traits that matter in the context of a specific interaction. To
201 overcome this obstacle, phylogenetic relatedness has been commonly used as a proxy
202 for similarity in traits or groups of traits between native and exotic species of plants or
203 herbivores (Becerra, 1997, Gilbert, Magarey, Suiter & Webb, 2012).
204 At a broad scale, related plant species may have similar defensive responses, and
205 exotic herbivore species closely related to native ones may share similar feeding habits.
206 Interestingly, a phylogenetically controlled comparative study of elicitors of plants
207 defences (FACs) showed that closely related species indeed have more elicitors in
208 common than species that are distantly related (Mori & Yoshinaga, 2011, Yoshinaga,
209 Alborn, Nakanishi, Suckling, Nishida, Tumlinson & Mori, 2010), suggesting evolutionary
210 conservatism of these cues. However, it remains largely unknown how different
211 assemblages of FACs interact and ultimately affect plant response for most herbivores.
212 In the context of understanding interference effects due to exotic herbivores on
213 infochemical networks, we speculate that the use of phylogenetic tools may be useful to
214 estimate the likelihood of an herbivore or a plant to possess certain traits, but will have
215 limited power to predict the outcome of a novel insect-plant interaction in terms of
216 production of specific plant volatiles after attack, and even less so how these volatiles
217 may interfere in the existing native interactions.
218
219 *Conceivable plant responses elicited by exotic herbivores*.

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Alternatively to a predictive, trait-matching approach, a more pragmatic approach may be taken to address the apparent "Pandora's box" of plant responses to novel herbivores. In the light of our knowledge of plant perception of herbivory, what general types of response can we expect from a plant in terms of divergence from its response to native herbivores? Intuitively, we can think of three possible types of response (Fig. 2): (1) *The null response*. The plant damaged by the exotic herbivore does not release volatiles that differ qualitatively or quantitatively from a mechanically wounded plant. This type of response is most likely to occur if the novel herbivore lacks the chemical elicitors present in the oral secretions of native herbivores. Examination of the elicitors present in a range of lepidopteran herbivores revealed that the most common elicitors (i.e. FACs structurally similar to volicitin) are not present in several species, supporting this notion (Yoshinaga *et al.*, 2010). In a controlled context, comparing the volatile blends emitted in response to plants mechanically wounded with and without oral secretions of the exotic species may be a good way to check whether the plant "reacts" to the novel herbivore. However, given the fact that repeated periodical wounding of a plant can be sufficient to elicit a response different from one-time mechanical damage (Mithöfer *et al.*, 2005), the null response may be hard to define under natural herbivore damage conditions.

(2) *The identical response*. The plant damaged by the exotic herbivore emits a blend of volatiles that is undistinguishable from the blend produced in response to a native herbivore. This type of response is more likely to occur if the exotic herbivore is closely related to the native herbivore and overlaps largely in terms of biochemical elicitors and feeding habits.

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(3) *The novel response*. The plant damaged by the exotic herbivore emits a blend that differs to some extent from the blends produced in response to its associated native herbivores. Any type of qualitative or quantitative change in the HIPV blend can theoretically be considered to have an element of novelty: even subtle differences in ratios of volatiles have been shown to impact the foraging behaviour of insects (Bruce *et al.*, 2005, Visser & Avé, 1978). The limited number of studies documenting induced direct defences of plants in response to exotic herbivores shows that different types of "novel responses" are possible, from reduced defensive response of the plant due to its evolutionary naiveté (Desurmont, Donoghue, Clement & Agrawal, 2011, Woodard, Ervin & Marsico, 2012), to an over-sensitive response to a particular herbivore (Radville, Chaves & Preisser, 2011).

The three theoretical types of responses to novel herbivory will have drastically different implications for insect-plant interactions, depending on the type of interactions that the plants have with the native insect (antagonistic or mutualistic), and on the degree to which native insects depend on HIPVs to achieve reproductive success. It is important to keep in mind that the distinction between an "identical" and a "novel" response ultimately depends on the level of chemosensitivity of the receiver, and to the degree of chemical complexity necessary to elicit a behavioural answer. An organism only able to detect (or only looking for) a reduced number of volatiles compounds may not distinguish between plants infested by a native and an exotic herbivore if the differences in HIPVs elicited by both herbivores are minor. On the other hand, organisms known to change their behaviour in response to subtle chemical changes, such as certain parasitic wasps, may be able to make this distinction. In other words, the same HIPVs blend emitted in response to an exotic herbivore may be perceived as an identical response or a novel response by different receivers.

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IS THERE ADAPTATION TO VARIATION IN HIPVS BY NATIVE INSECTS?

A wide range of insects belonging to different trophic levels and feeding guilds can perceive and make use of plant volatiles induced by herbivory (Dudareva, Negre, Nagegowda & Orlova, 2006, Hare, 2011), but the extent to which HIPVs can affect their reproductive success varies. For insect herbivores and pollinators, HIPVs may carry information regarding the quality of a plant as a resource (Cunningham, Moore, Zalucki & West, 2004, Fitt, 1989), which may result in adaptive attraction or deterrence, but herbivores and pollinators do not depend on HIPVs as long as they can locate suitable undamaged plants/flowers by using constitutively released plant volatiles or other cues, e.g. vision or vibration. On the other hand, specialized natural enemies such as parasitic wasps often rely on HIPVs as key foraging cues in detecting the presence of a host insect on a plant (Godfray, 1994, Quicke, 1997): their ability to detect suitable hosts ultimately determines their fitness. Indeed, parasitoids have been shown to possess a very strong innate propensity to respond to HIPVs (Vet, Lewis & Carde, 1995), as well as a strong capacity to learn novel odours (Turlings, Wäckers, Vet, Lewis & Tumlinson, 1993). Thus, some groups of insects have been under a stronger selective pressure to detect and respond to HIPVs than others, and these groups are at a greater risk to be significantly affected by disturbances in infochemicals caused by invasive herbivores. The other side of that coin is that insects that rely the most on HIPVs are also the most likely to have evolved adaptive responses to variation in HIPVs naturally occurring in their environment. For example, parasitic wasps may benefit from being able to find their hosts on plants growing under a range of environmental conditions, and thus to be adapted to variation in volatiles resulting from plant responses to different abiotic

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conditions (Chen, Schmelz, Wäckers & Ruberson, 2008, Gouinguené & Turlings, 2002, Winter & Rostás, 2010). Such adaptations could theoretically make them more "robust" to potential disturbance effects caused by invaders. In the following sections, we review the possible ecological consequences of HIPVs interferences for insects belonging to the different trophic levels involved in infochemical networks, and discuss their potential for adaptation to these disturbances.

INSECT HERBIVORES

Host plant location and acceptance by insect herbivores is typically performed by females, and plant chemistry plays an important role in these foraging efforts (Bernays & Chapman, 1994), not only aboveground but also belowground (Johnson & Nielsen, 2012). Detection of a suitable host-plant may depend on the recognition of specific chemical compounds (Blight, Pickett, Wadhams & Woodcock, 1995, Nottingham, Hardie, Dawson, Hick, Pickett, Wadhams & Woodcock, 1991), or of specific ratios of compounds (Visser & Avé, 1978). Many herbivore species prefer healthy unharmed plants of the appropriate species, but others prefer to deposit their eggs on plants that have already been damaged by conspecifics (Desurmont & Weston, 2011, Raffa *et al.*, 1993) or heterospecific herbivores (Poelman, Broekgaarden, Van Loon & Dicke, 2008, Shiojiri, Takabayashi, Yano & Takafuji, 2002). The use of HIPVs may be critical in distinguishing uninfested host plants from infested ones. For example, females of the moth *Heliothis virescens* are repelled by the emission of (Z)-3-hexenyl acetate and other aliphatic esters of (Z)-3-hexen-1-ol by caterpillar-infested tobacco plants, and prefer to deposit their eggs on unharmed plants (De Moraes *et al.*, 2001). Both attraction to and avoidance of infested plants can be adaptive for herbivores (Eigenbrode, Ding, Shiel & Berger, 2002),

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319 depending on whether the infested plant becomes more or less susceptible to
320 subsequent herbivory (Agrawal, 2000, Fordyce, 2003, Karban, Agrawal & Mangel, 1997).
321 Newly invading insects interfering with these volatile cues may lead to
322 maladaptive choices by native herbivores, such as attraction to plants with increased
323 resistance, or the avoidance of perfectly suitable plants. Oviposition "mistakes" (i.e.
324 phytophagous insects laying eggs on unsuitable plants) have received considerable
325 attention in the context of plant invasions (Harvey, Bukovinszky & van der Putten, 2010,
326 Harvey & Fortuna, 2012). Indeed exotic plants stimulating oviposition, but not
327 supporting offspring development, have been referred to as "ecological traps" for native
328 herbivores (Keeler & Chew, 2008). Here we advance the idea that exotic insect
329 herbivores may also lead to suboptimal feeding or oviposition choices and a degradation
330 of preference/performance relationships for native insects due to HIPVs interferences.
331 While such effects may naturally occur between pairs of native species within native
332 communities, we expect invasive exotic herbivores to have a greater disturbance
333 potential due to the lack of evolutionary history between the invader and native species.
334 Indeed native species may have evolved adaptive behavioural responses to HIPVs
335 associated with other native community members, but their responses to "novel" HIPVs
336 that result from unfamiliar herbivory are unpredictable and thus more likely to be
337 maladaptive. Ultimately, the realized fitness of native herbivores in presence and
338 absence of the exotic competitor will determine the strength and direction of the
339 selection imposed on the foraging behaviour of the native species.
340 The effects of HIPVs interferences on herbivores may extend beyond the infested
341 plant and reach neighbouring plants via plant-plant communication. Indeed, it is known
342 for several systems that plants can perceive and respond to HIPVs emitted by
343 conspecifics (Arimura, Ozawa, Horiuchi, Nishioka & Takabayashi, 2001) or other plant

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species (Karban, 2001), and use these infochemicals to induce or prime their own defences before herbivore attack (Heil & Karban, 2010, Ton, D'Alessandro, Jourdie, Jakab, Karlen, Held, Mauch-Mani & Turlings, 2007). Thus, HIPVs interferences have the potential to not only affect the foraging choices of native herbivores, but also, by changing the defence responses in neighbouring plants, affect herbivore performance and dispersal patterns at the patch level.

Are herbivores well-adapted to HIPVs variations in nature? It is generally assumed that specialized phytophagous insects have developed more finely-tuned interactions with their host plants, and may thus be capable of more complex or subtle choices when evaluating the quality of a resource. For example, the specialist elm leaf beetle *Xanthogaleruca luteola* is attracted to lightly infested elm leaves, but not heavily infested leaves (Meiners, Hacker, Anderson & Hilker, 2005). The same is true for the root-feeding larvae of the maize pest *Diabrotica virgifera virgifera*, which are attracted to already infested root systems, but not when infestation levels are high (Robert, Erb, Hibbard, French, Zwahlen & Turlings, 2012). For the viburnum leaf beetle *Pyrrhalta viburni*, both the magnitude of infestation (quantity of conspecifics' egg masses) and the quality of infestation (number of conspecifics that contributed to the infestation) have an effect on the oviposition preferences of females (Desurmont & Weston, 2010). On the other hand, generalist insect species are also capable of complex foraging decisions, as illustrated by grasshoppers mixing food sources in order to balance their dietary needs (Behmer, 2008, Behmer & Elias, 2000). Overall, there is no clear evidence that olfactory receptor neurons, which are the nerve cells used by insects to detect odours, differ in sensitivity or specificity between specialist and generalist insect herbivores (Bruce *et al.*, 2005). Therefore, diet breadth may not be a reliable indicator of how likely herbivores are to be sensitive or adapted to disturbances in HIPVs. In addition to innate preferences

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for certain volatiles, herbivores can also learn from previous experiences: food sources experienced as immature insects have been shown to affect the foraging preferences of adults in several systems (Akhtar & Isman, 2003, Webster, Qvarfordt, Olsson & Glinwood, 2013). Associative learning may thus help overcoming the potential detrimental effects of the presence of exotic herbivores for native species.

A key example of how chemically mediated interactions lead evolutionary trajectories of herbivores in a multitrophic context is given by the two lepidopteran species *Plutella xylostella* and *Pieris rapae*, which coexist on crucifer plants. Plants emit a different odour blend in response to damage by each of these herbivores. The parasitoid *Cotesia vestalis* is attracted by the odours of plants attacked by its host *P. xylostella*, but not by *P. rapae*, which is an unsuitable host and which it therefore does not attack. Females of *P. xylostella* appear to take advantage of that fact by preferring plants attacked by *P. rapae* for oviposition (Shiojiri *et al.*, 2002). These findings illustrate nicely that interference caused by an herbivore (i.e. *Pieris rapae*) on a volatile-mediated interaction (i.e. foraging behaviour of *C. vestalis* on crucifers) can have fitness consequences for a second herbivore (i.e. *Plutella xylostella*), leading to selection for an adaptive response to said interference in the long term.

INSECT POLLINATORS

Insect-pollinated plants rely on visual and chemical flower signals that help to optimize the attraction of effective pollinators (Fenster, Armbruster, Wilson, Dudash & Thomson, 2004). In many cases, volatiles produced by the flowers play an essential role in attracting pollinators from a distance, and convergent patterns in floral scents have been found among families of flowering plants (Raguso, 2008, Schiestl, 2010). Exotic

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herbivores may interfere with this mutualism if the feeding habits of the herbivore (e.g. florivory) directly impact the quality of the floral bouquet, or if plant volatiles emitted after herbivory affect pollinator attraction (Lucas-Barbosa, van Loon & Dicke, 2011). Direct herbivory on flowers has been demonstrated to affect visits by pollinators in several systems (Lohman, Zangerl & Berenbaum, 1996, McCall & Irwin, 2006). On the other hand, the effects of HIPVs emission on pollinator attraction vary: although lower visitation frequency on plants infested by herbivores seems to be the most common scenario (Adler, Karban & Strauss, 2001, Cardel & Koptur, 2010, Danderson & Molano-Flores, 2010, Kessler & Halitschke, 2009, Kessler, Halitschke & Poveda, 2011), higher pollinator attraction has also been documented (Poveda, Steffan-Dewenter, Scheu & Tscharntke, 2003). In wild radishes, uninfested plants were more visited by syrphid flies. This preference could not be linked to morphological features of flowers on infested plants (Lehtilä & Strauss, 1997), suggesting that avoidance of infested flowers is based on odorous cues. However, in most cases it is unclear whether the effect of HIPVs on pollination is due to a herbivore-induced volatile in the flower (Kessler & Halitschke, 2009) or to the reduction in the amounts of floral scents released by the plant upon herbivory (Kessler, Diezel & Baldwin, 2010). An interesting aspect is the possible compensation of herbivore-mediate reduction of floral attractiveness. A recent study with *Pieris brassicae* feeding on *Brassica rapa* suggests that plants compensate reduced attractiveness due to lower scent emission with the production of more flowers during early flowering (Schiestl et al in press). This compensatory plant response was not evident when the invasive *Spodoptera littoralis* was feeding on the plant, suggesting stronger fitness impacts of this herbivore-mediated through floral attractiveness to pollinators (Schiestl et al in review). On the long term, a trade-off between defence and reproduction can occur if herbivore-induced volatiles decrease pollination quality, or if

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floral odours interfere with the efficiency of volatile-mediated defences (i.e. attraction of herbivore antagonists). The outcome of these interactions for plant fitness will determine the direction of the investment toward reproduction or defence in presence of herbivores (Bartkowska & Johnston, 2012, Schiestl & Johnson, 2013).

What can we expect from pollinators in terms of adaptation to HIPV variation? As stated in the introduction, HIPVs may carry information about the quality of a resource to pollinators, such as the quality and quantity of the nectar reward (Kessler & Halitschke, 2007), but pollinators will rarely depend solely on the presence of HIPVs to find flowers. This consideration aside, it is well known that the main groups of generalist pollinators (honey bees, bumblebees) are remarkable learners (Riffell, 2011), using experience-based learning of olfactory and visual cues to exploit the most profitable nectar and pollen sources. They may thus be able to learn quickly whether a plant infested by an exotic species provides higher or lower quality reward compared to uninfested plants, and adjust their foraging preferences in accordance (Wright & Schiestl, 2009).

It is hard to predict which general type of plant response to novel herbivory (null, identical, or novel; Fig 2) is the most likely to have a significant impact on plant-pollinator interactions. We can only state that novel responses are the most likely to affect plant-herbivore-pollinator interactions in the invaded environment.

INSECTS FROM THE THIRD AND FOURTH TROPHIC LEVELS

As the third trophic level we consider the natural enemies of arthropods herbivores. They can be separated in two main categories: 1) predators, which feed upon a certain number of prey items during their lifetime, and, 2) parasitic wasps, flies, and a few

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444 species from other orders, also referred to as parasitoids, whose larvae develop on or
445 within eggs, larvae, or adults of insect herbivores, eventually killing their host. Insects
446 belonging to the fourth trophic level are natural enemies of predators and parasitoids.
447 The best-known insects belonging to the fourth trophic level are hyperparasitoids:
448 parasitic wasps that attack the larvae or pupae of primary parasitoids. In general,
449 parasitoids and hyperparasitoids are much more specialized than predators: they can
450 only parasitize a limited number of host species, less than the number of prey species
451 predators can attack. There are of course exceptions to that rule, and generalist
452 parasitoids and specialized predators are not uncommon (Hassell & May, 1986, Quicke,
453 1997).

454 In the search for prey or hosts, predators and parasitoids utilize cues that are
455 directly associated with the presence of hosts (Colazza, Cusumano, Giudice & Peri, 2014)
456 such as chemical traces left by insects' tarsi, frass, honeydew, or silk. These cues are
457 thought to be predominantly used for short-range foraging. To detect prey-infested
458 plants from a distance, natural enemies often rely on plant volatiles released locally and
459 systemically after herbivory (Vet & Dicke, 1992). How reliable are HIPVs as indicators of
460 the presence of specific herbivores on a plant? Reports on the subject (Clavijo
461 McCormick, Unsicker & Gershenzon, 2012, Dicke, 1999) indicate considerable variation
462 among systems. On one end of the spectrum, some plants release very similar blends of
463 volatiles in response to attacks by insects from different feeding guilds (Kessler &
464 Baldwin, 2001). On the other end of the spectrum, several plants have been found to
465 release distinct blends of volatiles in response to subtle changes in herbivore attack,
466 such as: developmental stage of the herbivore (Yoneya, Kugimiya & Takabayashi, 2009),
467 density of herbivores (Girling, Stewart-Jones, Dherbecourt, Staley, Wright & Poppy,
468 2011, Horiuchi, Arimura, Ozawa, Shimoda, Takabayashi & Nishioka, 2003), and whether

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herbivores have been parasitized or not (Poelman, Zheng, Zhang, Heemskerk, Cortesero & Dicke, 2011). Such specificity in volatile emission provides reliable information, which can be exploited by parasitoids to optimize their foraging decisions (Poelman *et al.*, 2011). In parallel, hyperparasitoids have recently been found to also use HIPVs to locate their parasitoid hosts. They are able to discriminate not only between plants bearing healthy herbivores and plants bearing parasitized herbivores, but also between plants with herbivores parasitized by their preferred host and plants with herbivores parasitized by a less optimal host (Poelman, Bruinsma, Zhu, Weldegergis, Boursault, Jongema, van Loon, Vet, Harvey & Dicke, 2012). These fascinating findings demonstrate that specific HIPVs can be exploited not only by natural enemies of insect herbivores, but also by the enemies of these enemies, and illustrate the complexity of HIPV-mediated multitrophic interactions.

In this context, volatiles emitted in response to exotic herbivores can interfere with the foraging behaviour of native insects from the third and fourth trophic levels in two main ways: 1) direct attraction to the plant damaged by the exotic herbivore only, and 2) increased or decreased attraction to plants infested by both the exotic herbivore and the native host or prey. The outcome of these two types of interferences on the fitness of predators/parasitoids/hyperparasitoids will also depend on whether the exotic herbivore can be successfully attacked or not. Exotic herbivores that cannot be attacked (=non hosts) constitute a 'dead end' for native natural enemies, and the attraction to plants infested by these non-hosts may be costly in time and energy. Such attraction to non-host infested plants has been documented for native parasitoids (Snoeren, Mumm, Poelman, Yang, Pichersky & Dicke, 2010). On the other hand, exotic herbivores that can be attacked may not negatively affect natural enemies through volatile attraction, but may allow native herbivores to escape predation/parasitism. The

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consequences of multiple herbivory (here, plants doubly infested with the native and the exotic herbivore) for parasitoids are much harder to predict and will be highly system-specific. This topic has been the subject of a recent review (de Rijk, Dicke & Poelman, 2013).

A recent study on the attraction of the predatory mite *Phytoseiulus macropilis* (Banks) illustrates how an uncommon herbivore can interfere with a chemically-mediated tritrophic interaction (Fadini, Venzon, Oliveira, Pallini & Vilela, 2010). It was found that the predator was strongly attracted to plants with the spider mite *Tetranychus urticae*, but avoided the odour of plants infested with the red mite *Oligonychus ilicis*. The former is a common, suitable prey for *P. macropilis*, the latter is not: *O. ilicis* is very rarely found on strawberry and usually does not occur in association with the predator. Doubly infested plants, carrying both herbivores, were not attractive to the predator, which supports the notion that interference in the chemical signalling by the unfamiliar herbivore may occur in this system (Fadini *et al.*, 2010).

Specific natural enemies such as the majority of parasitoids are short-lived organisms that often have a limited temporal and developmental window to find their hosts in an excessively complex olfactory landscape. Therefore, it can be expected that they have adapted, not only to the odorous cues betraying the presence of their host, but also to the potential disturbances in HIPVs that may naturally occur in the native environment. These adaptations can take two main forms: 1) A complex array of innate preferences for diverse blends of HIPVs reflecting adaptive choices toward reliable cues (Clavijo McCormick *et al.*, 2012), and 2) plastic preferences relying on associative learning to optimize foraging success (Vet & Dicke, 1992). Both of these adaptive strategies have been reported in predators (Glinwood, Ahmed, Qvarfordt & Ninkovic, 2011) and parasitoids (Geervliet, Vreugdenhil, Dicke & Vet, 1998).

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519 Finally, in terms of general plant response to novel herbivory (null, identical, and
520 novel) and realized impact on native organisms, we can make predictions for insects
521 belonging to the third and fourth trophic levels based on the notions developed through
522 this section. First of all, null plant responses are less likely to have an effect, as plant
523 responses to mechanical damage are usually less intense and less specific compared to
524 plants damaged by herbivores (Dudareva *et al.*, 2006, Wu & Baldwin, 2010), and
525 therefore likely to be less attractive to natural enemies. On the other hand, similarity in
526 response between plants infested by the exotic and the native herbivore may have
527 critical consequences for natural enemies if the exotic herbivore is a non-host. Indeed
528 identical responses would make plants infested by hosts and non-hosts
529 undistinguishable from a distance, with negative consequences for the foraging
530 efficiency of natural enemies potentially leading to local extinctions due to insufficient
531 parasitism rates (Vos, Berrocal, Karamaouna, Hemerik & Vet, 2001). Alternatively, if the
532 exotic herbivore can be attacked by natural enemies, then the presence of the exotic
533 herbivore on the plant may not negatively affect natural enemies but may still have
534 consequences for native predator-prey dynamics: on the one hand, native herbivores
535 may partially escape predation/parasitism if the exotic herbivore becomes a favoured
536 prey/host item. On the other hand, natural enemy densities may increase due to the
537 presence of the exotic herbivore as an alternative food, eventually negatively affecting
538 populations of native herbivores. Finally, the impact of novel responses cannot be
539 predicted and will certainly vary greatly among systems. The outcome will depend on
540 the compounds or ratios of compounds that constitute the elements of novelty of the
541 "exotic blend". In such cases of information disruption, the consequences for the natural
542 enemies will strongly depend on their behavioural plasticity and, on the long-term, on
543 their potential for rapid evolutionary adaptations.

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CONCLUDING REMARKS AND RESEARCH DIRECTIONS

Predicting insect-plant interactions in a rapidly changing world is a challenge that conservation ecologists are facing worldwide (Leimu, Muola, Laukkanen, Kalske, Prill & Mutikainen, 2012, Lürling & Scheffer, 2007, Pearse *et al.*, 2013, White, Wilson & Clarke, 2006). Thus far, the study of invasive species on community-level interactions has been largely confined to the effects of exotic plants on native plant assemblages (Callaway & Aschehoug, 2000, Keane & Crawley, 2002, Sakai, Allendorf, Holt, Lodge, Molofsky, With, Baughman, Cabin, Cohen & Ellstrand, 2001). The introduction of exotic herbivores or natural enemies can also seriously disrupt the functioning of native communities, with effects rippling through the food chain (Fortuna, Vet & Harvey, 2012, Kenis *et al.*, 2009, Pearson & Callaway, 2005). Although these direct and indirect effects of invasive species have been documented, we are not aware of any studies that have specifically addressed the effects of invading insect herbivores on the chemically mediated interactions among plants and native insects. In effect, the presence of an 'interloper' has the potential to diffuse or sever communication channels involving native herbivores, natural enemies, and pollinators, generating spatial asymmetries between different trophic levels that may destabilize tightly linked trophic interactions (Table 1).

Moreover, these effects on infochemical networks are likely to depend on the magnitude of the invasion: if the exotic herbivore becomes more abundant than natives, owing to release from its own specialized natural enemies, then it may exert a disproportionate effect on the native community by inflicting more damage on plants than the native herbivores. In this scenario, volatiles released from plants damaged by the invader may dominate the olfactory landscape, amplifying any interference effect

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569 caused by these HIPVs. In closely evolved systems, it can be expected that foraging
570 insects have adapted their responses to plant-emitted signals to optimize resource
571 location, and may thus have evolved some adaptive responses to volatile interferences,
572 but this question has not yet been considered in emerging theory of invasion biology.
573 Regarding the susceptibility of food webs to infochemical disturbances, it is
574 important to keep in mind that, due to domestication, crop plants may have lost some of
575 their ability to emit odorous distress signals in response to herbivory, as has been found
576 for modern varieties of maize that no longer emit root signals that attract
577 entomopathogenic nematodes (Degenhardt, Hiltpold, Köllner, Frey, Gierl, Gershenzon,
578 Hibbard, Ellersieck & Turlings, 2009, Rasmann, Köllner, Degenhardt, Hiltpold, Toepfer,
579 Kuhlmann, Gershenzon & Turlings, 2005) or no longer respond to freshly deposited
580 moth eggs that may enhance the plants responses to subsequent caterpillar feeding
581 (Tamiru, Bruce, Woodcock, Caulfield, Midega, Ogol, Mayon, Birkett, Pickett & Khan,
582 2011). This realization has motivated researchers to restore (Degenhardt *et al.*, 2009),
583 genetically alter (Kappers, Aharoni, Van Herpen, Luckerhoff, Dicke & Bouwmeester,
584 2005) or artificially enhance (Christensen, Nemchenko, Borrego, Murray, Sobhy, Bosak,
585 DeBlasio, Erb, Robert & Vaughn, 2013) the volatile emissions in crop plants. Thus,
586 agroecosystems often represent simplified olfactory landscapes compared to natural
587 environments, which may make them even more susceptible to interferences caused by
588 exotic herbivores.
589 Practically, experimental efforts should be made to understand the likelihood and
590 magnitude of disruption of infochemical networks by invasive insect herbivores. In the
591 context of insect invasions, the ecological effects of exotic HIPVs can only be tested by
592 combining careful examination of plant responses to insect invaders at the biochemical
593 level and manipulative experiments with native and exotic insects at the community

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level. In the end, measurements of fitness (or fitness correlates) of native insect species in presence and in absence of plant volatiles induced by the invader will be the most valuable indicator of the predicted impact of an invasive species as an "info-disrupter" on a given native environment.

Two challenges need to be considered by researchers investigating this topic. Firstly, because the effects of exotic species on the transfer of chemical information are likely to escalate through trophic levels via cascading effects (Harvey *et al.*, 2010), there is a wide variety of interactions involving native organisms that could potentially be impacted by a single invader, making the exhaustive examination of each of them extremely difficult. The challenge lies in determining which interactions should be examined with priority; these decisions should be based on the knowledge of the role and ecological functions of the native species involved in the system studied (Bukovinszky, van Veen, Jongema & Dicke, 2008). Secondly, measurements of fitness correlates of native organisms under controlled laboratory conditions, despite their usefulness, may have limited value compared to results obtained under field conditions. However, working with exotic species under natural conditions can only be done once the exotic organism has started invading the native environment, diminishing the value of risk assessments and impact predictions. To overcome this obstacle, researchers may take advantage of newly invaded environments to conduct field research in a still "naïve" ecosystem, and extrapolate results to areas at risk of being invaded in the future. This approach may be particularly valuable in the case of range-expanding species, owing to global changes such as global warming (Sorte, Williams & Zerebecki, 2010, Walther, Roques, Hulme, Sykes, Pyšek, Kühn, Zobel, Bacher, Botta-Dukát & Bugmann, 2009).

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992 **Tables**
993
994 **Table 1**. Examples of interferences in infochemical networks.
995

Type of interaction	Organisms involved	Origin of the interference	Result of the interference	Reference
Herbivore–herbivore and Predator-prey	Parasitic wasp-caterpillars	Native herbivore species	Presence of a non-host herbivore decreases the attractiveness of host-infested plants for the parasitic wasp. Host herbivores favour plant infested by the non host for oviposition.	Shiojiri et al. 2002
Predator-prey	Zooplancton - alga	Pollutant	Presence of a surfactant induces a costly anti-predator aggregation behaviour in a green alga	Lürling 2007
Predator-prey	Predatory mite – Spider mites	Uncommon herbivore species	Presence of the uncommon herbivore decreases the attractiveness of plants damaged by suitable prey	Fadini et al. 2010
Predator-prey	Parasitic wasp-caterpillar	Native herbivore species	Presence of a non-host herbivore increases the attractiveness of host-infested plants, but decreases the searching efficiency of the parasitoid.	Bukovinszky et al. 2012
Pollinator-flower	Wild tomato plants-bees	Native herbivore species	Plants damaged by herbivores show reduced attractiveness to pollinators and suffer reduced seed sets.	Kessler et al. 2011
Pollinator-flower	Wild radish-syrphid flies	Native herbivore species	Lower pollinator visitation rates on plants damaged by herbivores	Lehtilä and Strauss 1997

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998
999 **Figure legends**

1000 **Figure 1**. Illustration of how invasive insect herbivore may disrupt infochemical
1001 networks through interferences in herbivore induced plant volatiles (illustration by
1002 Thomas Degen).

1003 **Figure 2.** Illustration of conceivable plant responses to exotic herbivory**.** Letters
1004 represent volatile compounds emitted in response to mechanical damage or to feeding
1005 by two native herbivores. Three types of plant response to exotic herbivory are
1006 proposed. **Null response**: the blend emitted resembles the blend emitted after
1007 mechanical damage. **Identical response**: the blend emitted resembles the blend emitted
1008 in response to one native species (here, herbivore #1). **Novel response**: the blend
1009 emitted diverges from the blend emitted in response to native herbivores.

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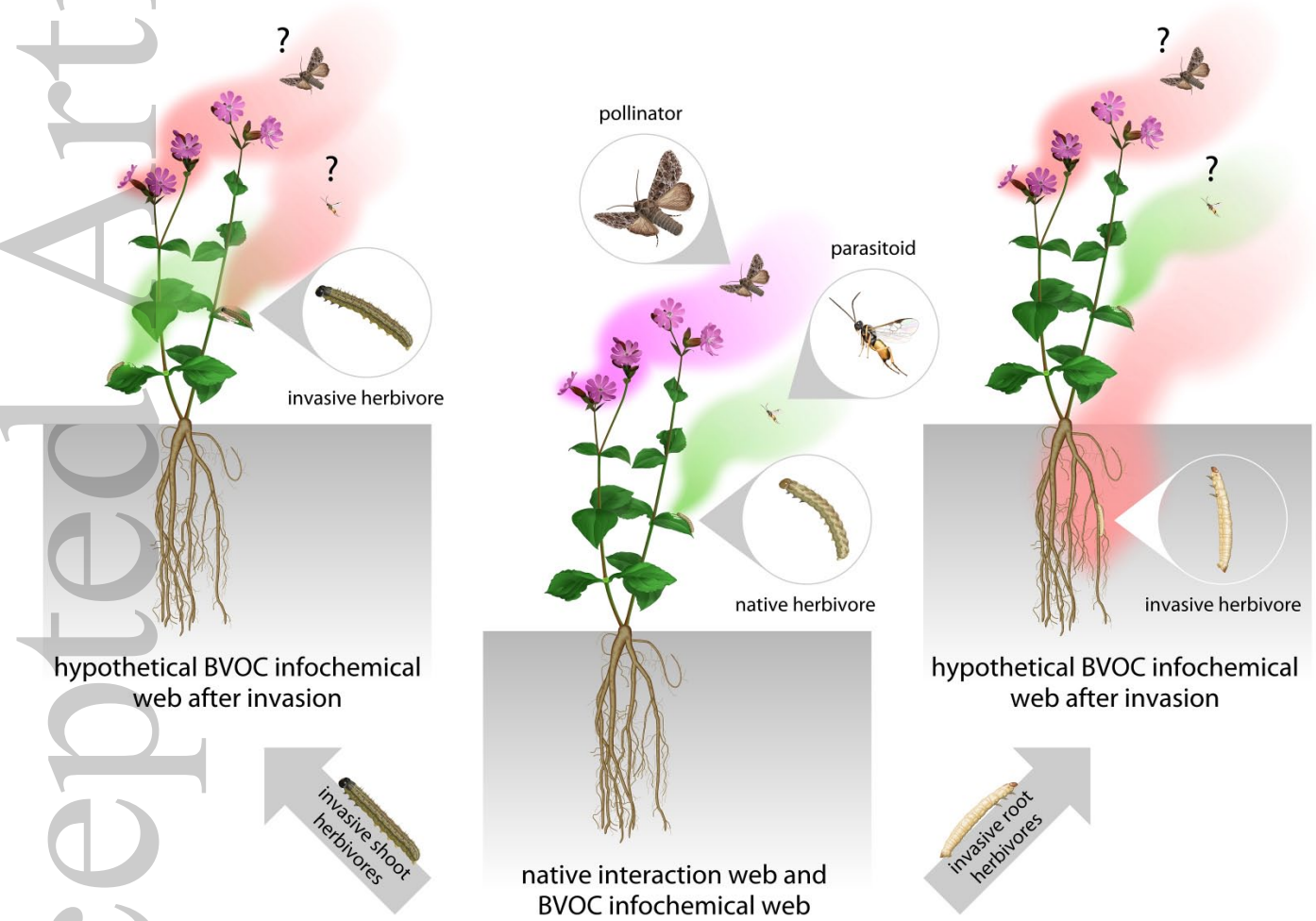

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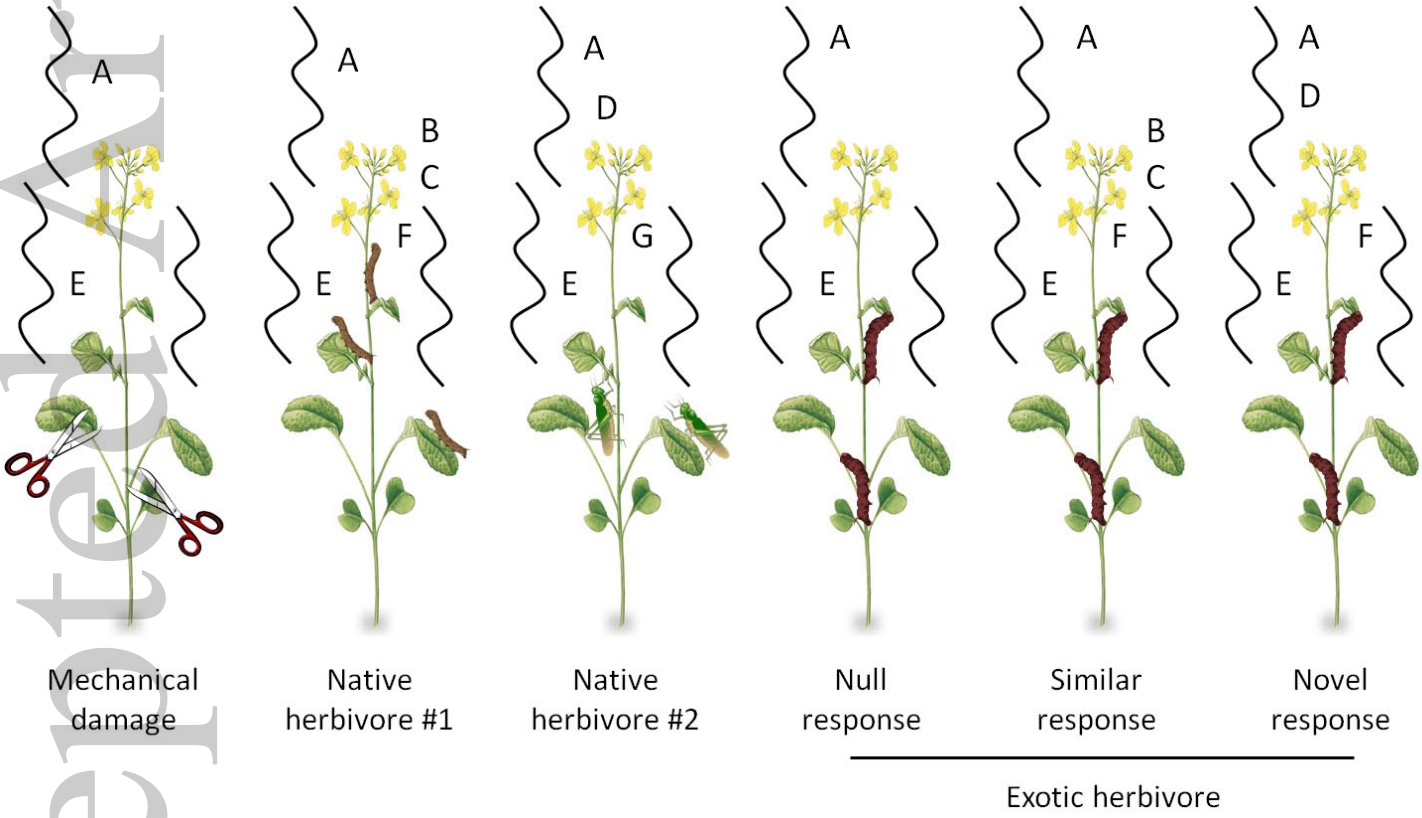

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